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TWO NEW FISHES OF THE MYCTOPHID GENUS *DIAPHUS* FROM THE ATLANTIC OCEAN

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No. 9 — *Two New Fishes of the Myctophid Genus* Diaphus *from the Atlantic Ocean*

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INTRODUCTION

During the course of a revisionary study of the myctophid genus *Diaphus*, representatives of two undescribed Atlantic species were found. These two, *Diaphus bertelseni* and *Diaphus lewisi*, are described below.

Of the few authors who have seriously studied *Diaphus*, a specialized myctophid offshoot, some thought it necessary to split the complex into various combinations of genera and subgenera (Goode and Bean, 1895; Fraser-Brunner, 1949; Bolin, 1939, 1959a). Others have maintained the vast array of species within the single genus *Diaphus* (Brauer, 1906; Tåning, 1918, 1928, 1932; Parr, 1928, 1929; Kulikova, 1961). I believe that the former approach has been adopted because of inadequate material and the taxonomic complexity of the group. For reasons which will be presented later in this paper, the inclusion of all the species (except two or, possibly, three) within the single genus *Diaphus* is followed here.

The taxonomic study of the "*Diaphus* complex" is not simple, but a reasonable approach can be made. Some of the difficulties involved are: 1) the close similarity among several species of the group; 2) the limited number of reliable diagnostic characters; 3) the relatively high degree of intraspecific variation; 4) the frail nature and generally poor state of preservation of these mesopelagic fishes; 5) the frequent differences between the luminous organs on the anterior part of the head (important diagnostic characters) of mature specimens and juvenile individuals of the same species; and 6) the sexual dimorphism frequently found in the size and occasionally in the number of these head luminous organs. As a result, the number of nominal species is now close to one hundred. We do not now know which of these are valid, but the number of synonyms may prove to be large.

Backus of the Woods Hole Oceanographic Institution (WHOI), Dr. William J. Richards of the Washington Bureau of Commercial Fisheries (WBCF), and Dr. Gerhard Krefft of the Institut für Seefischerei, Hamburg, have kindly provided material in their care. I am grateful to Dr. Rolf L. Bolin of Stanford University and Dr. Giles W. Mead of the Museum of Comparative Zoology (MCZ), Harvard University, for their kindness in reviewing the manuscript and for offering valuable advice and criticism. Partial financial support from National Science Foundation Grant GF 147 is gratefully acknowledged.

Abbreviations of names of luminous organs on the head, and of body photophores (Fig. 1), are as follows: Dn: dorsonasal; Vn:
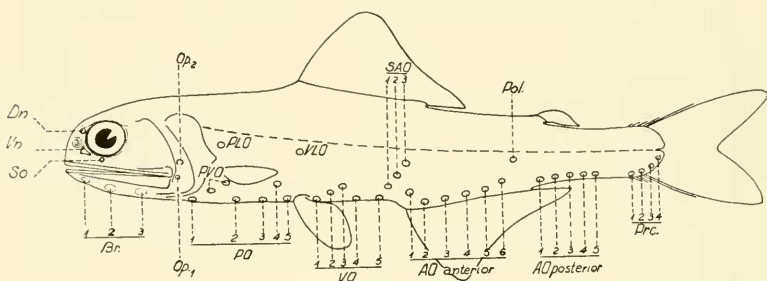

Fig. 1. Diagram of a generalized *Diaphus* showing distribution of the luminous organs of the head and body photophores. Abbreviations after Tåning, 1928, slightly modified.

ventronasal; So: suborbital; Ant: antorbital, a small triangular luminous organ present in several species and lying between the Dn and the anterodorsal aspect of the orbit, not shown in Figure 1; Br: branchiostegal; Op: opercular; PO: thoracic (or pectoral); PVO: subpectoral; PLO: suprapectoral; VO: ventral; VLO: supraventral; SAO: supra-anal; AOa: anterior anal; AOp: posterior anal; Pol: posterolateral; Prc: precaudal.

Measurements were made as follows: standard length (s. l.): shortest distance between tip of snout and end of hypural; head length: from tip of snout to extreme posterior margin of opercular flap; length of upper jaw: from anterior tip of premaxillary to its posterior end; eye diameter: horizontal distance between opposite margins of bony orbit; depth of head: vertical through posterior margin of orbit; depth of body: vertical through base of upper ray of pectoral fin; depth of caudal peduncle: least vertical depth; predorsal: shortest distance between tip of snout and origin of

dorsal fin; preventral: shortest distance between tip of snout and base of outermost ray of ventral fin; preanal: shortest distance between tip of snout and origin of anal fin.

All measurements were made with a pair of dividers and recorded in tenths of millimeters. Most measurements were made under a dissecting microscope. Initial values given in the lists of measurements are arithmetic means of all specimens measured; values within parentheses represent extremes. Methods of taking and presenting measurements conform to those used by Bolin (1939).

Diaphus bertelseni new species
Figures 2–5

Holotype.   A 49.0 mm standard length specimen, MCZ 43121, R/V CHAIN, WHOI, cruise 17, station RHB 801, 26 April, 1961, 00°15′S, 18°35′W to 00°15′S, 18°45′W, 10-ft. Isaacs-Kidd Midwater Trawl (IKMT), 0–85–0 m depth.

Paratypes.   One, 61.0 mm s.l., MCZ 43122, R/V CHAIN, WHOI, cruise 35, station RHB 971, 22 February, 1963, 02°00′S, 24°57′W to 01°48′S, 24°54′W, 10-ft. IKMT, 0–295–0 m depth.

Two, 21.0–23.0 mm s.l., Dana Collections, R/V DANA station 1223 V, 1 February, 1922, 22°06′N, 84°58′W, ring-trawl, open, conical net, 300 cm in diam. at opening (E300), 600 m wire out.

Additional material examined.   One, 9.8 mm s.l., R/V DANA station 1191 I, 14 December, 1921, 17°49′N, 64°54′W, 600 m wire out; one, 11.7 mm s.l., R/V DANA station 1231 II, 6 February, 1922, 24°30′N, 80°00′W, 600 m wire out; one, 8.5 mm s.l., R/V DANA station 1243 III, 16 February, 1922, 21°04′N, 73°48′W, 300 m wire out; four, 9.0–10.5 mm s.l., R/V DANA station 1256 IV, 4 March, 1922, 17°43′N, 64°56′W, 300 m wire out; one, 9.0 mm s.l., R/V DANA station 1257 IV, 6 March, 1922, 17°43′N, 64°56′W, 300 m wire out; one, 9.0 mm s.l., R/V DANA station 1274 III, 27 March, 1922, 17°43′N, 64°56′W, 600 m wire out. All these specimens were captured with stramin-nets, open, conical, 200 cm in diam. at opening (S200).

Description.   Body deep and short, its depth 3.5–3.8 in standard length; head large, its length 2.9–3.0 in standard length; diameter of eye 3.4–3.6 in length of head, 2.3–2.5 in length of upper jaw; length of snout equal to or slightly shorter than half the diameter of the eye; upper jaw 1.4–1.5 in length of head and extending less than one diameter of the eye behind posterior margin of orbit; posterior margin of operculum moderately pointed, the point
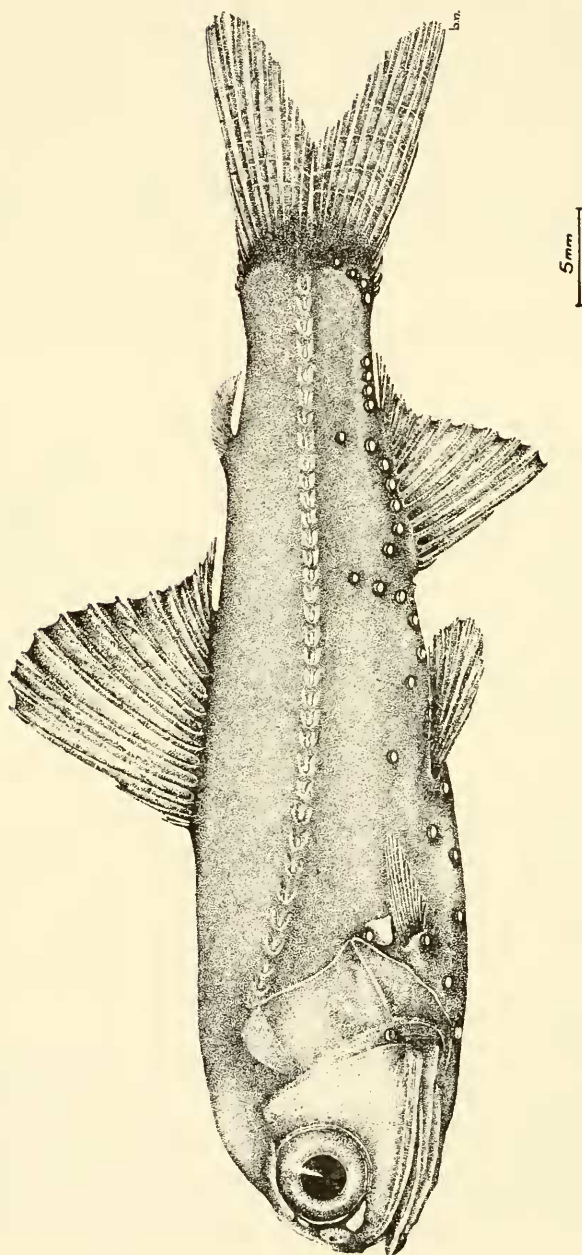
Fig. 2. *Diaphus bertelseni*, holotype, 49.0 mm standard length; R/V CHAIN, WHOI, cruise 17, station RHB 801, depth 85 m, MCZ 43121.

above PLO. Origin of dorsal fin somewhat anterior to base of ventral fin; origin of anal fin behind end of base of dorsal fin; pectoral fin short, its length 1.3 in distance between its base and that of ventral fin; ventral fin just reaching anus; adipose fin somewhat anterior to end of base of anal fin.

Luminous organs. Dn round, in cup-shaped recess, entirely above nostril and well separated from that of opposite side (Fig. 3);
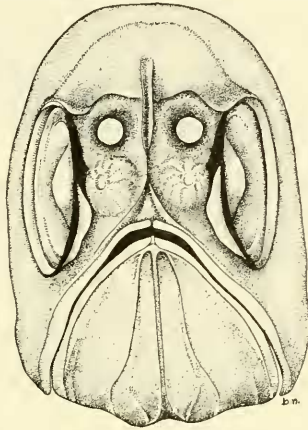

Fig. 3. *Diaphus bertelseni*, front view; semidiagrammatic representation of the luminous organs of the head.

Vn considerably larger than Dn, widest at anteroventral aspect of orbit, extending slightly around and under the nostril anteriorly, hardly reaching vertical through anterior margin of lens posteriorly. A conspicuous strip of darkly pigmented tissue present between anterior margin of orbit and luminous organs of head. Body photophores large, close to each other (particularly so in juveniles) and all well below lateral line; distance between PLO and lateral line $3-3\frac{1}{2}$ times the distance between PLO and base of upper ray of pectoral fin; distance between VLO and lateral line $2\frac{1}{3}-2\frac{1}{2}$ times the distance between VLO and base of outermost ventral fin ray; SAO equidistant from each other and on a straight, subvertical line; distance between lateral line and SAO_3 three times the diameter of that organ; AOa_1 elevated, its lowest margin on or slightly above line through upper margins of next two organs of same series; AOa_5 and AOa_6 on a gentle curve with Pol; distance between lateral line and Pol three times the diameter of that organ; AOp_1 above end of base of anal fin; Prc_4 slightly detached from rest

of organs in same series and well below lateral line. Large triangular luminous "scale" associated with PLO (especially well preserved on paratype, MCZ 43122).

Dentition. Both jaws with inner, irregular series of sharp teeth which are conspicuously larger than those in outer series; those on posterior part of premaxillary definitely curved forward (Fig. 4).
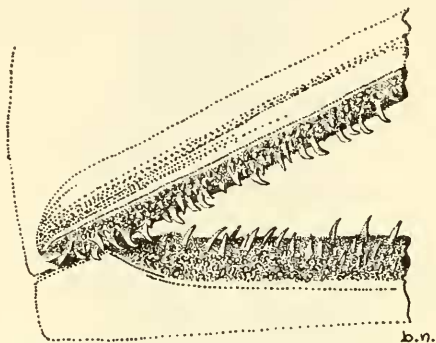

Fig. 4.   Lateral view (right side) of posterior parts of jaws, showing dentition in *Diaphus bertelseni* (from holotype).

Counts and measurements.   The data which follow are based on the holotype and the three paratypes. Data from non-type material are identified as such. Dorsal fin 14–15; anal fin 15; pectoral fin 11; ventral fin 8; gill rakers on first arch 5+1+12; scales in lateral line 34–35; AO 6 in anterior series and 4 in posterior series. Eight additional specimens, 8.5–11.7 mm s.l., had 6+4 AO, and a ninth had 7+3 on the left and 6+4 on the right side.

Measurements, in per cent of standard length, are as follows: length of head 34.4 (33.3–34.8); diameter of eye 9.9 (9.6–10.2); length of upper jaw 23.8 (23.0–24.4); depth of body 27.0 (26.0–28.5); depth of caudal peduncle 12.7 (12.2–13.0); predorsal 46.6 (44.9–47.8); preanal 69.9 (67.2–71.4); preventral 50.5 (48.4–52.4).

Affinities.   In general shape of body and in size and arrangement of photophores, *Diaphus bertelseni* (especially juveniles, Fig. 5) is quite similar to *D. brachycephalus* Tåning. This similarity is superficial, however, and there are many striking differences, such as the lack in *D. bertelseni* of a So, which is so prominent in *D. brachycephalus;* the number and arrangement of the AOa (6, with the first raised in *D. bertelseni*, as opposed to 5 in a straight line); the presence in *D. bertelseni* of a large luminous "scale" at PLO, the same structure being completely absent in Tåning's species,

which also possesses strongly curved and broad-based posterior premaxillary teeth.

Differences between *Diaphus bertelseni* and *D. coeruleus* (Klunzinger) are found primarily in the shape, size and position of the Dn; in the head and body dimensions (length of head 2.9–3.0 in standard length, as opposed to 3.5–3.7 in *D. coeruleus;* body depth 3.5–3.8 in standard length, as compared to 4.6–5.0 in *D. coeruleus*); in the length of the upper jaw which, in *D. bertelseni*, extends less than one eye diameter behind the posterior margin of the orbit, while in *D. coeruleus* "Upper jaw . . . hinder end . . . surpasses the eye by more than one eye diameter" (Weber and Beaufort, 1913, p. 169); in the number of AOp (4 in *D. bertelseni*, 5 in *D. coeruleus*).
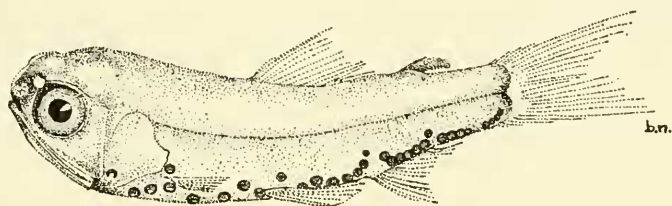

Fig. 5. *Diaphus bertelseni*, juvenile, 9.8 mm standard length; R/V DANA station 1191 I, 17°49′N, 64°54′W, 600 m wire out.

From *Diaphus taaningi* Norman, *D. bertelseni* differs mainly in the size and arrangement of photophores (larger and considerably further below lateral line in *D. bertelseni* than in *D. taaningi*), and in the number of organs in the AO series (6+4, as opposed to 5+5 in *D. taaningi*).

In all cases discussed above, differences in fin ray and lateral line counts are omitted as they are considered by the writer to be of minor diagnostic importance.

Distribution.   Pattern and limits of distribution of this species can not now be inferred. The positions of the few stations in which *Diaphus bertelseni* was taken (Fig. 6) suggest that the species is a South Atlantic one. Utilizing the South Equatorial Current, members of this group may enter the North Atlantic while remaining confined to the South Atlantic Central Water Mass. It is also possible that very young individuals are swept away from the northwestern boundaries of the South Atlantic Central Water Mass by the North Equatorial Current and are carried further west and north. The fact that only juveniles were taken in the Antillean and Florida waters, whereas the two south equatorial stations yielded adults, may be purely accidental.

This species is the same as that listed as *"Diaphus (sensu* Fraser-Brunner) sp. A"* by Backus et al., 1965.

The species is named in honor of Dr. E. Bertelsen, Director of the Danish Marine Biological Institute, Charlottenlund.
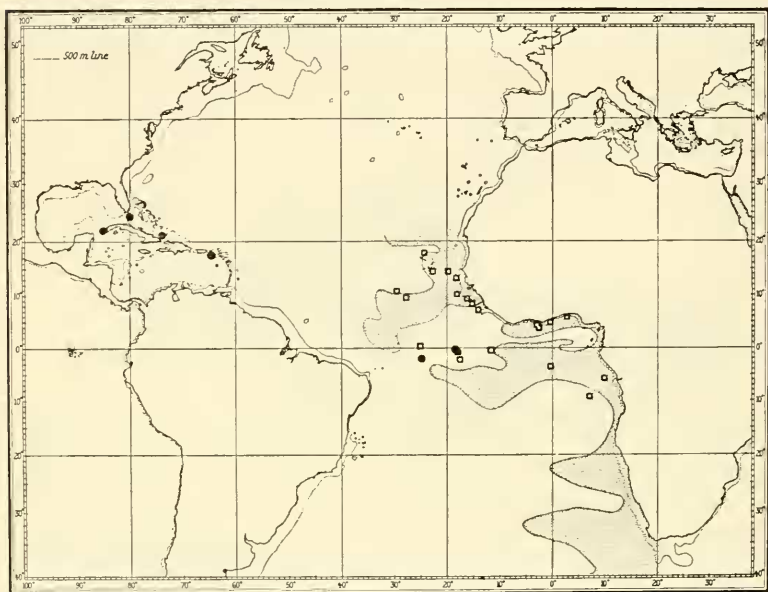

Fig. 6.   Chart showing the stations at which *Diaphus bertelseni* (solid dots) and *Diaphus lewisi* (rectangles) were taken. The solid dot at about 17°N, 64°W, represents four DANA stations (1191 I, 14 December, 1921; 1256 IV, 4 March, 1922; 1257 IV, 6 March, 1922; 1274 III, 27 March, 1922). Areas of high productivity are stippled (reproduced to scale from Sverdrup et al., 1942).

DIAPHUS LEWISI new species
Figures 7–11

Holotype.   Male, 27.5 mm standard length, Dana Collections, R/V DANA station 4005 XI, 12 March, 1930, 13°31′N, 18°03′W, stramin-net, open, conical, 200 cm in diam. at opening (S200), 50 m wire out.

Paratypes.   Two, 20.0–28.5 mm s.l., Dana Collections, data as above for holotype.

Four, 15.6–32.0 mm s.l., MCZ 44000, R/V CHAIN, WHOI, cruise 35, station RHB 972, 23 February, 1963, 00°03′N, 25°00′W to 00°15′N, 25°00′W, 10-ft. IKMT, 0–87–0 m depth.

One hundred, 18.5–31.8 mm s.l., R/V GERONIMO, WBCF, cruise 2, station 138, BCF Cat. No. 370, 19 August, 1963, 09°15′S, 07°06′E, mid-water trawl, depth (?). Eighty specimens in MCZ, MCZ 44001, 20 specimens in USNM, USNM 259155-F1.

Additional material examined. One, 22.0 mm s.l., R/V DANA station 1159 I, 29 October, 1921, 17°55′N, 24°35′W, ring-trawl, open, conical, 300 cm in diam. at opening (E300), 5000 m wire out; 133, 11.0–20.0 mm s.l., R/V DANA station 4003 VI, 9 March, 1930, 08°26′N, 15°11′W, stramin-net, open, conical, 150 cm in diam. at opening (S150), 1000 m wire out; one, 14.5 mm s.l., R/V DANA station 4004 IV, 11 March, 1930, 10°21′N, 17°59′W, stramin-net, open, conical, 200 cm in diam. at opening (S200), 100 m wire out; two, 25.0–26.8 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT4, 1 April, 1961, 02°10′S, 17°25′W, 10-ft. IKMT, 1800 m wire out; two, 23.0–25.2 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT5, 3 April, 1961, 00°35′S, 11°30′W, 10-ft. IKMT, depth (?); three, 15.2–15.7 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT9, 20 April, 1961, 07°15′N, 14°00′W, 10-ft. IKMT, 400 m wire out; one, 20.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 801, 26 April, 1961, 00°15′S, 18°40′W, 10-ft. IKMT, 0–85–0 m depth; three, 17.5–26.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 803, 1 May, 1961, 09°27′N, 27°45′W, 10-ft. IKMT, 0–275–0 m depth; 94, 10.2–26.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 804, 1–2 May, 1961, 10°55′N, 29°30′W, 10-ft. IKMT, 0–42–0 m depth; three, 25.5–28.7 mm s.l., R/V GERONIMO, WBCF, cruise 2, station 166, BCF Cat. No. 181, 25 August, 1963, 05°49′S, 10°00′E, mid-water trawl, depth (?); six, 21.5–29.0 mm s.l., R/V GERONIMO, WBCF, cruise 3, station 130, BCF Cat. No. 971, 26 February, 1964, 04°58′N, 00°30′W, mid-water trawl, depth (?); one, 23.5 mm s.l., R/V GERONIMO, WBCF, BCF Cat. No. 324, 03°28′S, 00°14′W; one, 30.0 mm s.l., R/V PILLSBURY, UMML, station 10, 25 May, 1964, 05°55′N, 02°52′E to 05°58′N, 02°50′E, IKMT, gear depth 0–655–1065–0 m; two, 15.0–18.0 mm s.l., R/V PILLSBURY, UMML, station 36, 29 May, 1964, 03°50′N, 02°37′W, IKMT, gear depth 0–750–0 m; one, 15.2 mm s.l., R/V PILLSBURY, UMML, station 37, 29 May, 1964, 04°00′N, 02°46′W to 04°05′N, 02°50′W, IKMT, gear depth 0–480–490–0 m; five, 23.5–26.8 mm s.l., R/V WALTHER HERWIG, Institut für Seefischerei, station 103, 24 March, 1964, 14°30′N, 22°45′W, IKMT, depth (?); one, 31.0 mm s.l., R/V WALTHER HERWIG, Institut für Seefischerei, station 109, 25 March, 1964, 14°30′N, 19°42′W, IKMT, depth (?); one, 29.2 mm s.l., R/V WALTHER

HERWIG, Institut für Seefischerei, station 129, 4 April, 1964, 09°14′N, 16°00′W, IKMT, depth (?).

Of the additional material examined, those specimens taken by R/V DANA are deposited in the Dana Collections, Charlotten-lund, Denmark; the specimens collected by R/V CHAIN and R/V GERONIMO are deposited in the MCZ; those caught by R/V PILLSBURY and R/V WALTHER HERWIG are to be found in the UMML and the Institut für Seefischerei, Hamburg, respectively.

None of the collections examined appears to have been made with closing nets.

Description. Small form; depth of body 3.8–4.3 in standard length; length of head 2.9–3.1 in standard length; diameter of eye 3.4–4.2 in length of head and 2.3–2.9 in length of upper jaw; snout longer than half the diameter of the eye; anterior spine-like end of supraorbital ridge extending forward and downward nearly reaching the posterodorsal aspect of the nostril; upper jaw 1.4–1.5 in length of head and extending one diameter of eye behind poste-rior margin of orbit; pterotic spine conspicuous; posterior margin of operculum rounded dorsally, moderately pointed posteriorly, the point at or slightly below PLO. Origin of dorsal fin directly above or slightly anterior to base of ventral fin; origin of anal fin behind end of base of dorsal fin; upper rays of pectoral fin reach base of ventral fin; ventral fin nearly reaching origin of anal fin; adipose fin above last 4–5 rays of anal fin.

Luminous organs. Dn apparently fused with Vn, the compound structure beginning at or somewhat higher than the dorsal margin of nostril, extending between latter and anterior margin of orbit and expanding ventrally, its posteroventral tip not reaching vertical through anterior margin of lens; a strip of black tissue separates the preorbital luminous complex from the anterior margin of orbit and extends along the ventral aspect of eye; its posterior end expands into a small pocket-like structure which protrudes into the iris behind the vertical through the middle of lens; inside the pocket-like structure there is a small, round So. The suborbital organ first appears in individuals 16.0–17.0 mm s.l., and in well preserved adult specimens it appears connected with the Dn-Vn complex by means of a very narrow isthmus of luminous tissue. Body photophores of medium size and separated from one another by an interspace at least as wide as the diameter of these organs; PLO and VLO distinctly closer to pectoral and ventral fin bases, respectively, than to lateral line; SAO series of three unequally
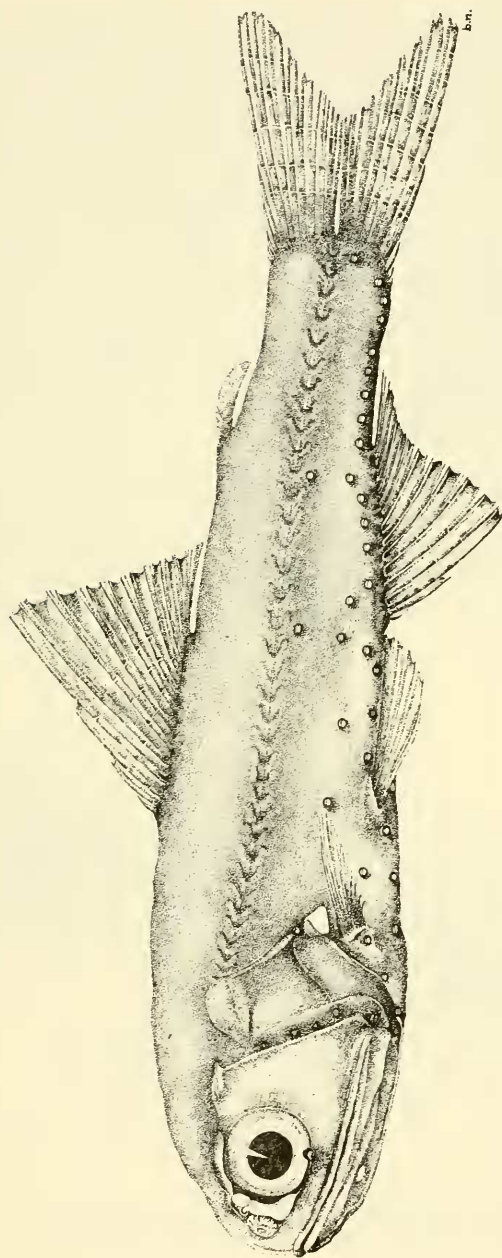
Fig. 7. *Diaphus lewisi*, holotype, male, 27.5 mm standard length; R/V DANA station 4005 XI, 50 m wire out. Dana Collections, Charlottenlund, Denmark.

spaced photophores forming a slightly curved and steeply ascending line; distance between SAO_1 and SAO_2 $1\frac{1}{2}$–2 times that between SAO_1 and VO_5, distance between SAO_2 and SAO_3 at least $1\frac{1}{2}$ times that between SAO_1 and SAO_2, SAO_3 about its own diameter below lateral line; AOa_1 1–2 times its diameter anterodorsad to AOa_2, last AOa in line with or slightly raised above preceding three or four organs of same series; Pol directly above last AOa and $\frac{1}{2}$–1 times its own diameter below lateral line; AOp_1 above posterior end of anal fin base; Prc_4 distinctly detached from rest of organs of same series and well below lateral line. A triangular luminous "scale" present at PLO.

Dentition. Upper jaw with inner series of strongly recurved, broad-based teeth (Fig. 8); lower jaw with inner irregular series of teeth feebler than those of upper jaw and only slightly curved forward.

Sexual dimorphism. Males are easily distinguished from females by the presence in the former of a conspicuous, roughly triangular antorbital luminous organ (Ant) immediately above and in contact with the Dn-Vn complex (Figs. 7 and 9). This sexual character first appears as a small, diffuse patch of luminous tissue in individuals 18.0–19.0 mm standard length, and attains its maximum size
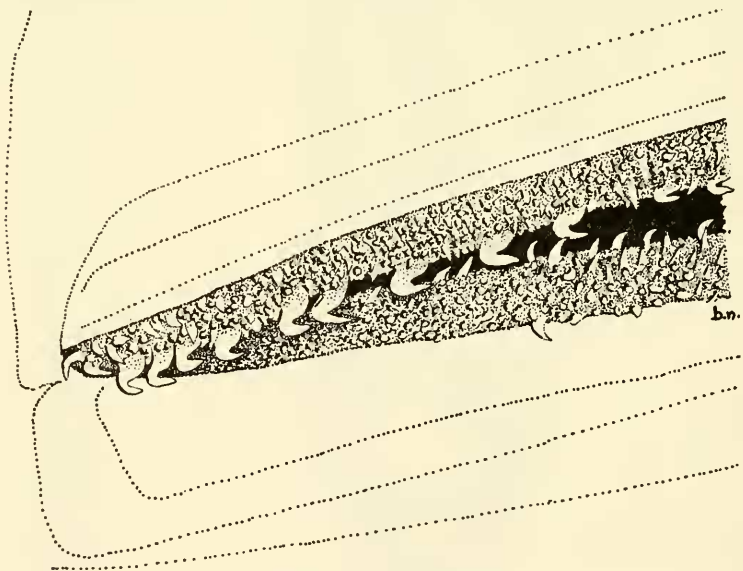

Fig. 8. Lateral view (right side) of posterior parts of jaws, showing dentition in *Diaphus lewisi*.

and its definitive outlines at sexual maturity which, in this small fish, is attained at a size of 27.0–28.0 mm standard length.

Counts and measurements. Meristic data based on 127 specimens are as follows: dorsal fin 13–14 (usually 14); anal fin 14–15 (usually 15); pectoral fin 10–11; ventral fin 8; gill rakers on first arch 7–8 + 1 + 14–15, total 22–24; scales in lateral line 35–36;
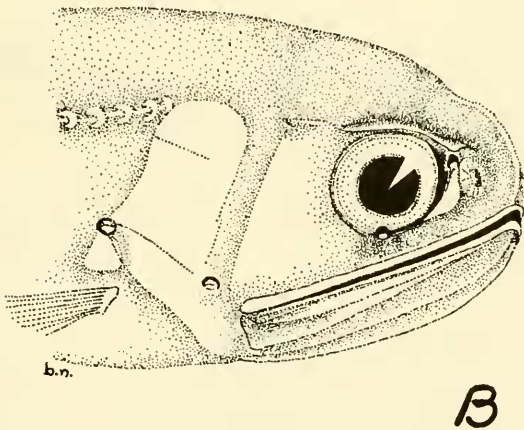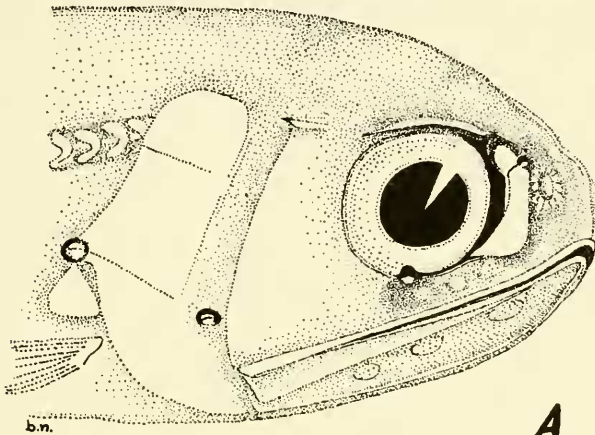

Fig. 9. Sexual dimorphism in the luminous organs of the head in *Diaphus lewisi*. A: male, 32.0 mm standard length; B: female, 27.0 mm standard length.

AOa 5–6 (very rarely 7), AOp 4–5 (very rarely 6). The AO series show considerable variation in number and arrangement not only among individuals but also between two sides of the same individual, the most common patterns being those shown in Figures 7 and 10.
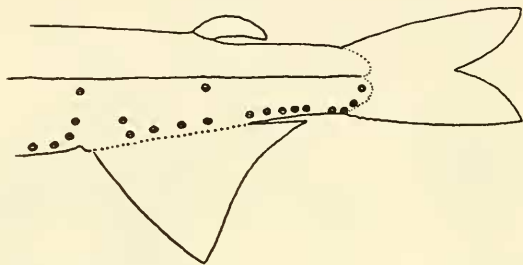

Fig. 10. Caudal region of *Diaphus lewisi*, showing variation in the number and arrangement of the photophores in the AOa series.

Measurements, in per cent of standard length, based on 40 specimens 15.6–32.0 mm s.l., as follows: length of head 33.6 (32.1–35.0); diameter of eye 8.9 (8.1–10.3); length of upper jaw 23.3 (22.0–24.2); depth of body 24.4 (23.0–26.2); depth of caudal peduncle 10.9 (10.0–12.6); predorsal 46.5 (44.8–48.9); preanal 65.4 (62.0–67.0); preventral 47.1 (44.8–48.5).
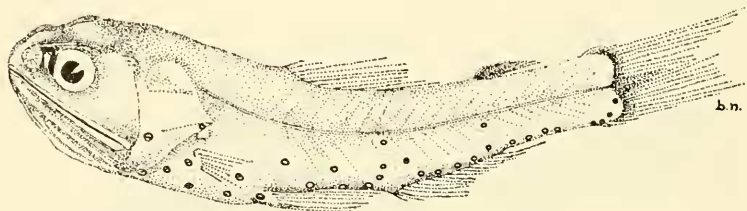
Fig. 11. *Diaphus lewisi*, juvenile, 11.5 mm standard length; R/V CHAIN, WHOI, cruise 17, station RHB 804, 10°55′N, 29°30′W, depth 42 m.

Affinities. *Diaphus lewisi* is a small fish, probably not growing larger than 32–33 mm in standard length. It belongs to the *Diaphus rafinesquei* group which includes *D. rafinesquei* (Cocco) and *D. holti* Tåning in the northeastern North Atlantic, *D. mollis* Tåning, *D. brachycephalus* Tåning, and probably *D. theta* Eigenmann and Eigenmann in the southwestern North Atlantic and, in

addition, several other species elsewhere. The main characters common to the members of this group are the three distinct luminous organs on the head (Dn, Vn and So) and the strongly recurved, broad-based premaxillary teeth. *D. lewisi*, although deviating from the typical *rafinesquei* pattern of luminous organs on the head in the fusion of the Dn and Vn, does possess the peculiar premaxillary dentition characteristic of the group.

Diaphus suborbitalis Weber from the Indo-Pacific area has luminous organs on the head which seem to be intermediate between those of the *rafinesquei* group and those found in *D. lewisi*. In Weber's species the Dn and Vn tend to, but have not fused completely. In many other respects *D. suborbitalis* is, according to Weber (1913, p. 91), closely related to *D. fulgens* Brauer, a typical species of the *rafinesquei* group from the Pacific Ocean and one possibly identical with *D. mollis* Tåning. Further discussion of possible relationships among the species mentioned in this paragraph must await a direct comparison of pertinent material.

Distribution. Available data suggest that the area occupied by *Diaphus lewisi* is rather well defined (Fig. 6). Within its range this species is quite common, and the pattern of its distribution is obviously influenced by the hydrography along the west coast of Africa. The cold Benguela Current and the continuous upwelling from depths of 200–300 m account for the remarkably high productivity, the relatively low temperature, and the low salinity of the coastal surface water. These conditions stand in contrast to those of surface waters of the general South Atlantic tropical and sub-tropical areas which are warmer, more saline and low in nutrient content (Raymont, 1963). The belt of fertile water extends approximately 200 km offshore, forming tongues of gradually diminishing plankton density extending outward from the coast (Fig. 6). These tongues correspond to the main water movements that flow away from the coast, as indicated by the outward extension of the isotherms (Sverdrup et al., 1942). The high productivity of the coastal Benguela Current is reflected in the rich zooplankton with which, in turn, may be associated the abundance of marine vertebrate and invertebrate forms (Raymont, 1963).

With a knowledge of the hydrography of the area concerned, the distribution of *Diaphus lewisi* and, no doubt, of other mesopelagic forms becomes meaningful. Relatively abundant along the continental slope of the African west coast and particularly so in areas of high productivity, *D. lewisi* becomes less and less common towards the west. The northernmost limits of its distribution

(about 18°N) more or less coincide with the southern limits of the North Atlantic Central Water Mass. A rather marked drop in water temperature at about 18–20°S and in depths of 200–400 m possibly constitutes a barrier to the spreading of the species further south along the west coast of Africa.

The species is named in honor of Dr. Robert E. Lewis, Curator of the Museum of Natural History, American University of Beirut, Lebanon.

DISCUSSION

Taxonomy. The taxonomy of the "*Diaphus* complex," like that of other difficult groups, has been arranged and repeatedly re-arranged, especially on the generic level, with little success in achieving a stable system. Inadequate material may have been one of the main reasons for the existence in the literature of so many genera and subgenera. With the increase in the number and size of collections, some students of this group began realizing that they were dealing with the potentially unlimited inventiveness of nature as regards the size, shape and complexity of the luminous organs of the head. They also saw that such morphological features as the "theta" (Greek letter θ) configuration of the body photophores and the number and arrangement of some of the series of these organs (PVO, PO, VO and Prc) seemed, with very few exceptions, highly constant throughout the group. As a result one single genus, *Diaphus*, was accepted and used by them.

Myctophid taxonomy has been heavily dependent on the number and distribution of photophores. It is undoubtedly true that these characters are of great importance in distinguishing the genera within the family. However, at the species level the value of these characters is often questionable. Their inadequacy, in the *Diaphus* group at least, becomes obvious as one grows familiar with: a) the close morphological similarity shown by several species of the group, and b) the relatively high degree of intraspecific variation which often masks interspecific differences.

In contrast to the generally conservative diaphid morphology, the luminous organs of the head show an astonishing variety of sizes, shapes, patterns and numbers. In most cases the role of these organs in interspecific differentiation is decisive.

Of the few diagnostically important characters available to the student of the *Diaphus* group, some have been consistently overlooked. To cite one example: In most studies of *Diaphus* very little, if any, attention has been paid to dentition, a character the

importance of which has been repeatedly emphasized by Bolin (1939, p. 124; 1959, p. 20). In his detailed description of the genus *Diaphus*, as exemplified by *Diaphus rafinesquei*, Bolin (1939, p. 124) calls attention to the peculiar dentition of this species and suggests that: "Probably most of the other species now placed in the genus will require re-allocation since examination of several forms has failed to reveal a dentition similar to that found in *Diaphus rafinesquei*."

Bolin's suggestion subsequently found support in the observation that those forms with sharply recurved premaxillary teeth also had three well-defined luminous organs on the head (Dn, Vn and So). These two features, namely dentition and pattern of luminous organs, seemed important enough to justify generic distinction of the species which possessed them. However, further examination of large numbers of specimens belonging to different diaphid species has revealed that the premaxillary teeth display a series of gradually changing shapes. Between the two extremes, straight and sharply recurved, there exists a series of more or less curved premaxillary teeth. Furthermore, the young of some species (e. g. *Diaphus elucens*, *D. problematicus*, etc.) have curved teeth, especially on the posterior end of the premaxillary. These teeth are apparently lost and replaced by straight or less-curved ones in older individuals of the same species. Finally, a generic line becomes even more difficult to draw if one considers the existence of forms like *Diaphus lewisi* and, probably, *D. suborbitalis* Weber. The former species (I have not personally examined *D. suborbitalis*, hence I cannot speak with certainty about it), while deviating considerably from the *rafinesquei* pattern of luminous organs on the head, does show the *rafinesquei* kind of dentition.

The gradual change in shape displayed by the premaxillary teeth does not at all diminish the diagnostic usefulness of dentition, especially in the case of juveniles of morphologically very similar diaphid species. Young individuals of *Diaphus fragilis* Tåning and *D. elucens* Brauer, for instance, are very difficult to differentiate. With the numbers and arrangement of their body photophores strikingly similar, luminous organs of the head easily confused (before attainment of their definitive pattern and size), and with horizontal distributions considerably overlapping, the juveniles of these two species can be identified on the basis of premaxillary and particularly dentary teeth shape and size (e. g. lower jaw with inner series of very large, widely but regularly spaced teeth in *Diaphus fragilis*, lower jaw with inner irregular series of denser and much smaller teeth in *D. elucens*).

Turning once again to the character of the luminous organs of the head, we are faced with a situation somewhat analogous to that of the teeth. These organs, in their great variety of designs, can, with some imagination, be arranged in one or more series of progressively increasing complexity. This has certainly been attempted in the past (Parr, 1928, p. 140). However, sound inferences about evolutionary trends of these organs cannot be made on the basis of external morphology alone. A careful histological study of their structure and innervation could probably help us gain some insight into the evolution of the numerous patterns and thus, perhaps, lead us to a better understanding of the phylogenetic relationships among the various species in the group.

Professor Rolf Bolin is of the opinion (personal communication) that there are several divergent lines within the *Diaphus* group. Although I fully agree with his opinion, I feel inclined to disagree with the idea that these divergent lines are, at the present state of our knowledge at least, clear enough to justify a division of the group into more than two genera. An attempt to formalize these lines would lead either to a large number of genera or, at best, to a reasonable number of genera but with several species "suspended" in between. On the basis of the arguments presented above, it is suggested here that all but the species assigned to the genus *Lobianchia* Gatti (e.g. *Aethoprora* Goode and Bean, *Panthophos* Jordan and Hubbs, *Lamprossa* Jordan and Hubbs, *Cavelampus* Whitley) be included within the single genus *Diaphus*, without formal division into subgenera (e.g. *Hyperphotops*, *Panthophos* and *Lamprossa*, all three erected by Fraser-Brunner in 1949).

Ecology, speciation and phenotypic similarity. Some speculation on the phenotypic similarity among several myctophid forms is in order here, and should start with a brief consideration of some aspects of oceanic ecology and of possible ways of speciation among high-seas forms. Ecological conditions in the sub-tropical and tropical oceans seem to have been quite stable in geological time (Marshall, 1963, p. 182). Relative differences in physicochemical factors, i. e. temperature, salinity and density, between adjacent water masses and, below the thermocline, between bathymetrically contiguous layers are usually very small. Repeated invasions of these adjacent environments by populations of a given species probably result in some of the more adaptable individuals becoming physiologically adjusted to the small differences. Following this adjustment, which may not require more than slight adaptive changes in the reproductive physiology of the invaders,

colonization of the new habitat, or habitats, is under way. Subsequently, one might expect the gene flow between the colonizers and the parent species to decrease. Finally, perhaps through the development of preferential mating and competition ". . . between [the] contiguous populations in the zone of contact and the subsequent elimination of the less well adapted intermediates in this zone. . . ." (Ebeling, 1962, p. 149, from Fryer, 1959), the initial, partial isolation of the populations may be substantially reinforced. Now, if this is the approximate sequence and extent of the major evolutionary events leading to the formation of new species, then it would be reasonable to infer that speciation in many deep-sea fishes does not necessarily involve conspicuous or even readily noticeable structural modifications.

In considering the great morphological similarity among several myctophid forms one should also take into account such evolutionary processes as convergence and parallel adaptations. Hubbs (1941, p. 190) says: "The general tendency of fishes to speciate along parallel courses in correlation with the temperature and salinity of the water is being repeatedly indicated. . . ." Finally, in his discussion of the phenomenon of sibling species, Mayr (1963, p. 57) calls attention to the evidence, found in recent work in developmental genetics, indicating that there is a selective premium on the maintenance of the phenotype. "Any disturbance of the developmental process by a gene mutation will result in a selection pressure in favor of other genes that restore development along the normal, time-tested channels" (Mayr, 1963, from Lerner, 1954, and Waddington, 1956).

The rather strong emphasis placed above on adaptation to apparently minor differences in physico-chemical factors seems to be in conflict with the known ability of adult myctophids to tolerate wide extremes in temperature, salinity and, perhaps, several other ecological factors. In the course of their extensive (several hundred meters) diurnal vertical migrations, these fishes "may well be subjected to much greater differences in temperature than those marking the limits of their distribution" (Fraser-Brunner, 1949, p. 1020). This conflict may be resolved if we assume that during a certain period, or periods, of the year these fishes become, in terms of reproductive physiology, specifically stenothermal and stenohaline. It may also be that survival of the gametes, successful fertilization, or early development fail in the absence of optimal, species-specific physico-chemical conditions. If these assumptions are correct we should expect these optimal

ecological conditions to delimit the breeding area and hence the distribution of the species. But, "certainly in the sea we have many suggestions that the distribution of the species is much wider in many instances than the distribution of the breeding population" (Ebeling, 1962, p. 139, from Bullock, 1958). This brings us to another potent environmental factor, namely the oceanic current patterns, and their role in the phenomenon of "expatriation."

Expatriation. Within a breeding area the larvae are restricted to surface or near-surface waters. Just before, or at the very beginning of metamorphosis, these larval forms move to deeper layers. Based on his studies of larval fishes, Tåning (1918, p. 20) writes: "There can . . . hardly be any doubt that the Scopelids [myctophids], when metamorphosis sets in, undergo a thorough change, acquiring a different specific gravity to that which they had as postlarvae, and consequently move down, either actively or passively, to water layers of a specific gravity suitable to their requirements during metamorphosis, and later, after the metamorphosis is completed, ascend once more to the upper layers. In other words, we have here a decided instance of (passive or active) ontogenetic migration." Both as larvae prior to their "ontogenetic migration" and as young right after their ascent to the upper layers, myctophid and other forms with similar life histories are at the mercy of the prevailing current systems in the area concerned. The larvae and young may either be carried away from the breeding area or they may be kept restricted within it (current gyres, eddies, etc.). In the first case the individuals may spread over a wide range, far away from the breeding area of the species to which they belong. Sexual maturity will probably be attained while in environments which, although favorable in terms of satisfaction of purely individual needs, are far from meeting the species-specific reproductive requirements. These individuals are thought to be "expatriated" and reproductively lost to their populations (Ebeling, 1962, p. 139).

Concerning the fate of the "expatriates," Ekman (1953, p. 317) remarks that ". . . it remains questionable whether the species is able to exist independently in the unfavorable region or whether it would not die out there if it were not continuously reinforced from the more favorable regions," and ". . . the unfavorable region is . . . outside the real home of the species, and it [is] . . . possible to contrast the autochthonous main mass of the species which lives in the reproductive area with an allochthonous sterile expatriated contingent in an expatriation area." Bolin (1959b,

p. 142), also, points out that "while straggling adults may exist for long periods in waters far beyond the normal range of the species, permanent populations are restricted to the proximity of the areas where spawning can be successful." During my study of the distribution of the diaphid species in the Atlantic Ocean I have found considerable evidence indicating that many of the diaphid specimens captured off the northeastern coast of the United States are "expatriates" belonging to species the breeding areas of which are well within the tropical and sub-tropical waters.

I am well aware of the weaknesses in my assumptions and arguments. I would like to conclude with a well-worn but nevertheless appropriate statement — a great deal of work remains to be done, especially with regard to the distribution and bionomics of this scientifically and, perhaps, economically important group of mesopelagic fishes.

LITERATURE CITED

BACKUS, R. H., G. W. MEAD, R. L. HAEDRICH and A. W. EBELING
 1965. The mesopelagic fishes collected during cruise 17 of the R/V Chain, with a method for analyzing faunal transects. Bull. Mus. Comp. Zool., **134**(5): 139–157.

BOLIN, R. L.
 1939. A review of the myctophid fishes of the Pacific coast of the United States and of lower California. Stanford Ichthyol. Bull., **1**(4): 89–160.
 1959a. Iniomi. Myctophidae from the "Michael Sars" North Atlantic deep-sea expedition, 1910. Rep. "Michael Sars" N. Atl. Deepsea Exped., **4**(7): 1–45.
 1959b. Differential bipolarity in the Atlantic and Pacific as expressed by the myctophid fishes. *In* International Oceanographic Congress, Preprints, 31 August – 12 September 1959, Mary Sears, ed., American Association for the Advancement of Science, Washington, D. C., pp. 142–143.

BRAUER, A.
 1906. Die Tiefsee-Fische. I. Systematischer Teil. Wiss. Ergeb. Deutsch. Tiefsee-Exped., Valdivia, 1898–99, **15**, 432 pp.

EBELING, A. W.
 1962. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana-Report No. 58, 1962, Carlsberg Foundation, Copenhagen, 164 pp.

EKMAN, S.
 1953. Zoogeography of the sea. Sidgwick and Jackson, London, 417 pp.

FRASER-BRUNNER, A.
 1949. A classification of the fishes of the family Myctophidae. Proc. Zool. Soc. London, **118**: 1019–1106.

GOODE, G. B. and T. H. BEAN
   1895. Oceanic ichthyology. Special Bull. U. S. Nat. Mus., Washington, XXXV + 553 pp.
HUBBS, CARL L.
   1941. The relation of hydrological conditions to speciation in fishes. Symp. Hydrobiol., Univ. Wisconsin Press, pp. 182–196.
KLUNZINGER, C. B.
   1870. Fische des Rothen Meeres. I. Theil. Percoiden-Mugiloiden. Wien, 248 pp.
KULIKOVA, E. B.
   1961. On the lantern fishes of the genus *Diaphus* (Scopelidae) from the western Pacific. Trudy Inst. Okeanol. Moskva, **43**: 5–39. (In Russian.)
MARSHALL, N. B.
   1963. Diversity, distribution and speciation of deep-sea fishes. *In* Speciation in the sea, J. P. Harding and Norman Tebble, eds., Symp. Syst. Ass., Pub. 5, London, pp. 181–195.
MAYR, E.
   1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Massachusetts, 797 pp.
NORMAN, J. R.
   1930. Oceanic fishes and flatfishes collected in 1925–1927. Discovery Repts., Cambridge, **2**: 261–370.
PARR, A. E.
   1928. Deep-sea fishes of the order Iniomi from the waters around the Bahama and Bermuda Islands. Bull. Bingham Oceanogr. Coll., New Haven, **3** (Myctophidae): 47–156.
   1929. Notes on the species of myctophine fishes represented by type specimens in the United States National Museum. Proc. U. S. Nat. Mus., **76**: 1–47.
RAYMONT, J. E. G.
   1963. Plankton and productivity in the oceans. Pergamon Press, Macmillan Co., New York, 660 pp.
SVERDRUP, H. U., M. W. JOHNSON and R. H. FLEMING
   1942. The oceans, their physics, chemistry and general biology. Prentice-Hall, Inc., New Jersey, 1087 pp.
TÅNING, Å. V.
   1918. Mediterranean Scopelidae. Repts. Danish Oceanogr. Exped. 1908–10, Kjøbenhavn, **2**: 1–154.
   1928. Synopsis of the scopelids in the North Atlantic. Vidensk. Medd. Dansk. Naturh. Foren. Kbh., Kjøbenhavn, **86**: 49–69.
   1932. Notes on scopelids from the Dana expeditions. Vidensk. Medd. Dansk. Naturh. Foren. Kbh., Kjøbenhavn, **94**: 125–146.
WEBER, M.
   1913. Die Fische der Siboga-Expedition. Siboga Repts., Leyden, **57** (32): XII + 710.
WEBER, M. and L. F. BEAUFORT
   1913. The fishes of the Indo-Australian archipelago. Leyden, **2**: XX + 404.